fashion as if there were machines on an assembly line" (p. 44). Rich designated these groups *polyribosomes* or *polysomes*. To his characterization of the polysomes as constituting assembly lines, he quickly noted a difference between the ribosomal assembly line and human ones: "the polyribosome is not the usual kind of assembly line. In such an assembly line, the product moves down the line and component parts are added to it. In the polyribosome assembly line the ribosomes move down the line and each one makes a complete product."[34]

Evidence for polysomes came in two forms. The first were fractionation studies with rabbit reticulocytes, which are cells lacking a nucleus and specialized for manufacture of hemoglobin. Rather than using a medium of constant density, Rich centrifuged the contents in a solution spatially graded from 15% to 30% sucrose. Examination of the ultraviolet absorption characteristic of RNA in the centrifugation product revealed peaks in two fractions – one that corresponded to single ribosomes and the other to heavier materials, presumably polysomes. The amino acids in the preparation were labeled with C^{14}, making it possible to identify materials in which protein synthesis was occurring, and this showed a single peak corresponding to the polysome fraction. This suggested that the polysome was the locus of protein synthesis, a conclusion that was further supported by the fact that applying ribonuclease to the medium before centrifugation resulted in no fraction corresponding to polysomes and the radioactivity being transferred to the single ribosome fraction.

Rich collaborated with electron microscopists to develop a second form of evidence for polysomes. Using metal shadowing, the resulting electron micrographs clearly revealed clusters of ribosomes. In collaboration with Henry Slayter at MIT he used positive staining with uranyl acetate to develop micrographs that also revealed a thread 10 to 15 Å in diameter running between the ribosomes, which corresponds to the estimated thickness of a single strand of RNA. Calculating the diameter of the five polysomes attached to the thread and the gap between them resulted in a length of 1,500 Å, the expected length

[34] Rich seemed quite concerned with the appropriateness of the analogy. He returned to it again later in the paper and commented, "It is evident that protein synthesis is not really an assembly line process as it is normally understood. It would be more appropriate to compare protein synthesis with the operation of a tape-controlled machine tool. The tool will turn out an object of any shape within its range of capabilities, in response to information coded on the input tape. In factories where such tools are used each tool is provided with its own tape, but if it served any purpose a single tape could easily be fed through a battery of identical tools. The living cell evidently makes one tape serve for many tools because this is an efficient way to do the job" (pp. 50–1).